Oviposition vs. offspring fitness in *Aphidius colemani* parasitizing different aphid species

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Abstract

We measured the acceptance and suitability of four aphid species [*Aphis gossypii* Glover, *Myzus persicae* (Sulzer), *Rhopalosiphum padi* (L.), and *Schizaphis graminum* (Rondani)] (Homoptera: Aphididae) for the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae). Female parasitoids parasitized fewer *R. padi* than the other three aphid species, and fewer offspring successfully completed development in *R. padi* than in the other three host species. Sex ratios of emerging adults were more male-biased from *R. padi* than from the other three aphid species, suggesting that *R. padi* is a poor quality host for this population of *A. colemani*. Ovipositing *A. colemani* encountered *R. padi* at a slower rate, spent more time handling *R. padi*, and parasitoid offspring died at a higher rate in *R. padi* compared to *A. gossypii*. Our results show that oviposition behavior and offspring performance are correlated. In each experiment, we tested the effect of the host species in which the parasitoids developed (parental host) on the number of hosts attacked, the proportion of each host species accepted for oviposition and the survival of progeny. Parental host affected maternal body size and, through its effect on body size, the rate of encounter with hosts. Other than this, parental host species did not affect parasitism.

Introduction

Studies of host range can provide insight into the trade-offs associated with specialization and into speciation via host-race formation (Futuyma & Moreno, 1988; Thompson & Pellmyr, 1991). Individuals with a broad host range have an advantage over those with a narrow host range because they can switch host species when one host becomes difficult to find. However, many species are highly specific in their use of hosts; thus the challenge is to explain why the host ranges of such species are not broader. Most theories concerning specialization in host use assume there are trade-offs between host range and host-use efficiency (Via & Lande, 1985; Lynch & Gabriel, 1987). Specialists are often more efficient at host location or better able to cope with host defenses than generalists, but specialization may come at the cost of being poorly adapted to other host species. Because of such trade-offs, specialist parasites whose development is intimately tied to host physiology are more likely to have highly restricted host ranges.

Studies of host range and host use efficiency are also important for applied pest management. The success and safety of biological control introductions depend on an ability to predict post-introduction host use. Many pest populations are ephemeral; populations of natural enemies that can switch successfully to alternative host species may persist better and provide control when pest populations resurge (e.g., DeBach & Rosen, 1991; Pike et al., 1999). On the other hand, knowledge of the behavioral and physiological bases of host use will help in assessing the potential for deleterious impacts on non-target species, an increasingly contentious issue in biological control (Simberloff & Stiling, 1996; Hopper, 2000).

Experimental studies of the trade-offs associated with the use of different host species, especially those focusing on trade-offs within a parasite species, are rare (Futuyma

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& Moreno, 1988) and this is particularly true for parasitic wasps (Godfray, 1994). Compared to many predators, parasitic wasps (parasitoids) have narrow host ranges, presumably because parasitoid development is often intimately associated with the physiology and immune responses of their hosts. This is thought to be especially true of parasitoids that allow their hosts to continue development (koinobionts) and develop internally (endoparasitoids) (Askew & Shaw, 1986; Strand, 1986). Yet, even among koinobiotic endoparasitoids, host range varies widely. Several species of aphelinid and braconid parasitoids, including *Aphidius colemani* Viereck (Hymenoptera: Braconidae), are known to attack as many as 60 species from several aphid genera (Stary, 1975, 1983; Kalina & Stary, 1976; Mescheloff & Rosen, 1990; Hopper et al., 1998; Takada, 1998). However, some extremely polyphagous species appear to be composed of distinct host races that rarely switch between host species in the field (Nemec & Stary, 1983; Stary, 1983; Cameron et al., 1984; Tardieux & Rabasse, 1986, 1990; Powell & Wright, 1988; Messing & Rabasse, 1995; Atanassova et al., 1998; Takada & Tada, 2000). While much is known about the relationship between host use and offspring fitness within a host species (Godfray, 1994), less is known about the relationship between host use patterns and offspring performance across host species. In two studies, there was a positive association between host acceptance by the ovipositing mother and larval survivorship. In a study of *Asobara tabida*, a parasitoid of drosophilids, van Alphen & Janssen (1982) showed that ovipositing females were more likely to reject a host species in which larval survival was low. In a series of host choice tests using *Monoctonus paulensis*, an aphid parasitoid, ovipositing females were most likely to accept aphid species with the greatest likelihood of producing adult offspring (Chau & Mackauer, 2001).

In this paper, we measured the behavioral and developmental differences in the parasitic wasp, *A. colemani*, when exposed to four host aphid species. By directly observing whether an egg is laid at each encounter with a host, we assessed host acceptance by the ovipositing female as well as progeny survival. We measured the relationship between oviposition and offspring survival among host species, which is key to demonstrating adaptive host use. We also examined whether host species influences offspring sex ratio. Ovipositing females may allocate sons and daughters differentially in different host species; alternatively, sons and daughters may survive differently when developing in different host species. A female's pattern of oviposition may depend primarily on the host species she encounters, or she may exhibit a higher acceptance rate of the same host species in which she developed (Vet & Groenewold, 1990; Godfray, 1994). We consider both possibilities.

Materials and methods

We used *A. colemani* from a colony established from approximately 1000 wasps received from Bio-Bee Biological Systems insectary, Sde Eliyahu, Israel, in September 1999. These wasps had originally been collected from *Aphis gossypii* on cucumber (*Cucumis sativus* L.) in Israel, and had been insectary-reared on *A. gossypii* on cotton for 10 years (approximately 260 generations) with annual infusions from field collected material. We maintained our aphid populations at high levels throughout the experiments. We therefore do not believe that inbreeding had a significant impact on our results. We subcultured these wasps on the following four aphid species with the indicated host plants: cotton aphid, *Aphis gossypii* Glover, on cotton (*Gossypium hirsutum* L.); green peach aphid, *Myzus persicae* (Sulzer), on radish (*Raphanus sativus* L.); bird cherry-oat aphid, *Rhopalosiphum padi* (L.), on barley (*Hordeum vulgare* L.); and greenbug, *Schizaphis graminum* (Rondani), on barley. We focused our studies on these four aphid species because they are agronomically important and abundant pests from which *A. colemani* is commonly collected in the field in Israel (Mescheloff & Rosen, 1990). Two species, *R. padi* and *S. graminum*, were reared on the same host plant species, allowing us to control for the effect of host plant when comparing the host use of these two species. We used no-choice tests because female *A. colemani* foraging in the field are unlikely to encounter more than one aphid species during the short exposure periods used in our experiments.

Patterns of use among four aphid species
To measure differences in use of these four aphid species by our study population of *A. colemani*, we exposed females from each subculture to each of the four aphid species. This experiment was conducted 6–8 generations after the *A. colemani* population was subcultured on each aphid species. We isolated mummified aphids containing *A. colemani* from each subculture. As female wasps emerged, we allowed them to mate with a single male from their own subculture for 24 h. A subset of five mated females were dissected from each subculture and examined for sperm in their spermathecae. Sperm was present in the spermathecae of all females, suggesting that all females used in this experiment were inseminated. One-day-old, mated females from each of the four subcultures were put individually into cages with a plant infested with approximately 100 aphids of one of the four species. Thus, there were 16 treatments (four parental host species × four exposure host species). Each combination was replicated 6–10 times. Cages were 2 l clear plastic cylinders on 10 cm diameter pots containing either cotton infested with

Table 1 Mean (± SEM) proportion of 3rd instars, 4th instars, and adults among the aphids used as hosts in the host use experiments. Aphid dry mass is based on five replicates of 10 individuals each. Different letter superscripts on the dry mass values are significantly different (Fisher's LSD test)

| Species | Aphid stage | | | Dry mass (mg) |
	3rd instar	4th instar	Adult	
A. gossypii	0.105 ± 0.01	0.831 ± 0.008	0.064 ± 0.010	0.019[c]
M. persicae	0.064 ± 0.010	0.859 ± 0.012	0.076 ± 0.009	0.048[a]
R. padi	0.122 ± 0.016	0.839 ± 0.017	0.037 ± 0.012	0.029[b]
S. graminum	0.081 ± 0.011	0.875 ± 0.016	0.044 ± 0.010	0.025[b]

A. gossypii, radish infested with *M. persicae*, barley infested with *R. padi*, or barley infested with *S. graminum*. Females were exposed to aphids for 1 h, after which time they were removed from the cage, frozen, dried for 48 h at 50 °C, and weighed to the nearest 0.001 mg with a Mettler Toledo UMT2 microbalance (Mettler Toledo, Columbus, OH, USA). The exposed aphids were held in plant growth chambers under a photoperiod of L16:D8 and at 22 °C for 10 days (i.e., until mummies formed). The numbers of mummified aphids in each cage were counted, and after emergence, the adult wasp offspring were sexed and counted. Aphid age and size distribution at the time of parasitism was estimated from five additional cages for each of the four aphid species. Approximately 100 randomly selected aphids from each cage were categorized by instar. In all trials, at least 80% of the aphids at the time of parasitism were fourth (last) instar. The remaining individuals were adults and third instars (Table 1). The aphid size (dry mass) of each species was measured by collecting 10 individuals from each of five cages, drying them at 50 °C for 48 h, and weighing them to the nearest 0.001 mg (Table 1). We used an ANCOVA to test the joint effects of parental host and exposure host on the number of mummies formed, the number of adults that emerged, and the sex ratio of the emerged adults. We used maternal dry weight as a covariate because the effect of parental host might arise from the effect of aphid species on maternal body size.

Acceptance and suitability of two aphid species

In the above experiment, it was not possible to follow female behavior consistently in the cages. Therefore, we could not determine whether differences in the numbers of offspring among aphid species reflected differences in host acceptance (i.e., oviposition) or in host suitability (i.e., progeny survival). To resolve this issue, in a second experiment, we followed individual females in Petri dishes under a stereomicroscope at 30× magnification, recording each time a host was encountered and each time an egg was laid. To assess our ability to reliably predict if an egg was laid during each host encounter, we observed a total of 304 female wasps encountering a single host (of one of the four aphid species) and recorded whether an egg was laid

or the host was rejected. A female who rejected a host, often explored but never punctured the cuticle of the aphid with her ovipositor. Approximately half of the aphids were dissected immediately after the encounter with the wasp and carefully examined for the presence of an *A. colemani* egg; the other half were dissected 3 days later and examined for *A. colemani* larvae. While we were unable to find eggs in some of the hosts in which we observed an oviposition, we never found an *A. colemani* egg or larva in a host that we observed to be rejected (Table 2). We concentrated on differences in the acceptance and suitability of *A. gossypii* and *R. padi* because they showed strong differences in host use in the first experiment, and were the dominant aphid species on cotton and wheat, respectively, in the field in Israel. In addition to exposing wasps from *A. gossypii* and *R. padi* to each of these hosts, we included wasps from *S. graminum* because these wasps developed on the same host plant but a different aphid species and thus allowed us to test the response to parental host species independent of response to host plant species. This

Table 2 Interpretation of host encounter outcomes in *Aphidius colemani* as a function of aphid species. Each observed host encounter was recorded as accepted (one egg laid) or rejected (no eggs laid). 'n' is the number of females observed to accept or reject a single host aphid. Approximately half of the aphids were dissected immediately after being encountered by a wasp and examined for the presence of an *A. colemani* egg (no. with eggs present/total no. aphids accepted or rejected). The other half were dissected 3 days later and examined for the presence of an *A. colemani* larva

| Host species | Observation | n | Dissection results | |
			Day 1	Day 3
A. gossypii	Accepted	52	22/25	25/27
	Rejected	17	0/8	0/9
M. persicae	Accepted	64	26/31	30/33
	Rejected	23	0/10	0/13
R. padi	Accepted	48	20/24	18/24
	Rejected	34	0/16	0/18
S. graminum	Accepted	53	23/25	27/28
	Rejected	13	0/6	0/7

experiment was conducted about 14 generations after we established subcultures on each aphid species.

We isolated 31 mummified aphids containing *A. colemani* from subcultures on *A. gossypii* (n = 6), *R. padi* (n = 7), and *S. graminum* (n = 18). As the females emerged, each was exposed to a single male from their own subculture for 24 h. Then, we randomly placed each female individually in a 10 mm diameter Petri dish containing either 15 *A. gossypii* (n = 14) on a cotton leaf or 15 *R. padi* (n = 17) on a barley leaf. Only fourth instar aphids were used in these experiments. While directly observing wasp behavior, we recorded the number of hosts encountered, the number of hosts parasitized, the time spent handling hosts (including antennation, probing, and oviposition), and the total time elapsed from the first host encountered to the last host attacked. Each female was followed until she had oviposited in 10–12 hosts. Female wasps were then frozen, dried for 48 h at 50 °C, and weighed. As each host was parasitized, it was removed and replaced with an unparasitized host so that each female wasp had access to 15 unparasitized hosts at all times. Parasitized hosts were placed on either cotton (*A. gossypii*) or barley (*R. padi*) and held in plant growth chambers under a L16:D8 photoperiod and at 22 °C until mummies formed. We recorded the number of mummies that formed, the number of adult offspring that emerged, and the number of males vs. females among the offspring. This design enabled us to measure the rate of encounter with hosts, the handling time per host, the proportion of hosts accepted for oviposition, the proportion of parasitized hosts that produced mummies and adult offspring, and the proportion of males among the adult offspring. We used an ANCOVA to test the effects of parental host and exposure host on each of these measurements. Because the effect of parental host might arise from the effect of aphid species on maternal body size, we used maternal dry mass as a covariate in these analyses.

Results

Host use: number of mummies and adults, parental body size, and offspring sex ratio

The species of aphid exposed to *A. colemani* females affected the number of adult offspring that emerged (type III $F_{3,93} = 32.4$, P<0.001). Fewer adult offspring emerged from *R. padi* than from *A. gossypii*, *M. persicae*, or *S. graminum* (Figure 1). The host species in which *A. colemani* females were reared affected their mass (type III $F_{3,107} = 43.4$, $R^2 = 0.55$, P<0.001); females from *M. persicae* were larger than those from *R. padi*, which, in turn, were larger than those from *S. graminum*, which were larger than those from *A. gosspyii* (Figure 2; Fisher's LSD: t = 1.98, P<0.05). Similarly, unparasitized *M. persicae* were significantly
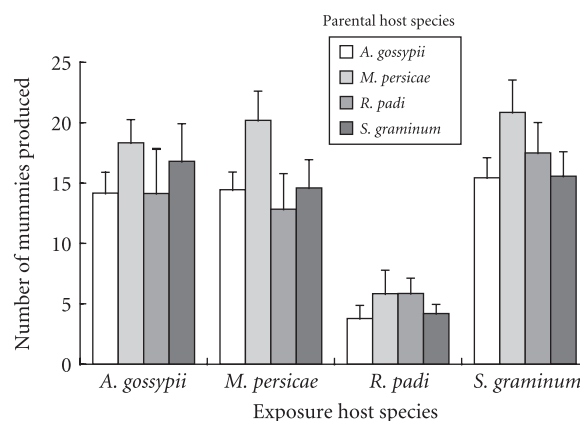

Figure 1 Number (mean + SE) of adult offspring produced by *Aphidius colemani* reared on various host species (parental host) for six generations and then allowed to parasitize one of four host species (exposure host) ($F_{16,93} = 7.16$, P<0.0001; see text for source effect type III F-statistics).

heavier than *S. graminum* and *R. padi*, which in turn were heavier than *A. gossypii* (Table 1; $F_{3,16} = 45.61$, P<0.001). However, neither the host species in which parents developed nor the maternal mass affected the number of adult offspring (respectively, type III $F_{3,93} = 1.58$, P = 0.20; and type III $F_{1,93} = 0.000068$, P = 0.99). Furthermore, the host species in which the parents developed and the species in which the offspring developed did not interact in their effects on the number of adult offspring (type III $F_{9,93} = 0.46$, P = 0.90).

Exposure host affected the proportion of males among adult offspring (type III $F_{3,87} = 3.56$, P = 0.02); the proportion of males was higher for *R. padi* than for *A. gossypii*, *M. persicae*, or *S. graminum* (Figure 3; Fisher's LSD: t = 1.99, P<0.05). Neither the host species on which parents developed nor the maternal dry mass affected the proportion of
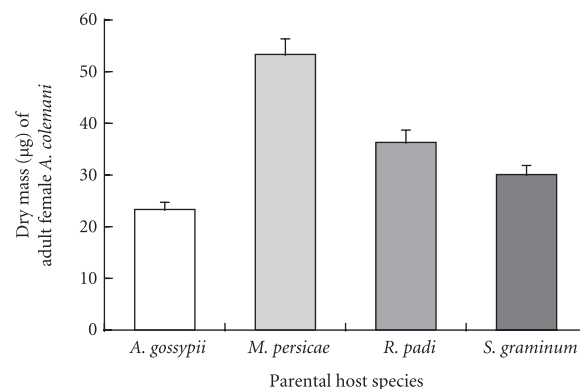

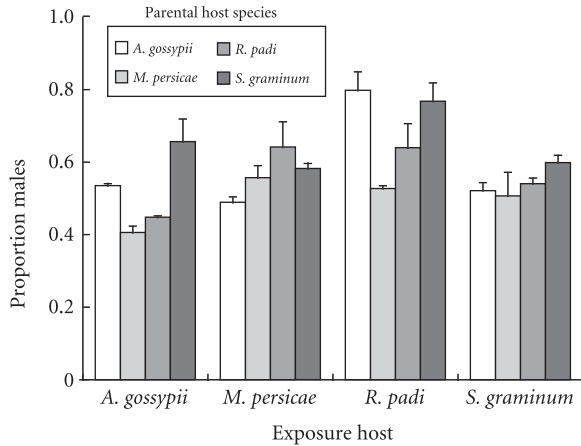**Figure 2** Effect of parental host on *Aphidius colemani* female dry mass (µg; mean + SE).

Figure 3 Sex ratio (mean + SE; back transformed from arcsine square root transformation) produced by *Aphidius colemani* females reared on one of four host species (parental host) on each of four host species (exposure hosts).

males among adult offspring (type III $F_{3,87} = 1.36$, P = 0.26 and type III $F_{1,87} = 0.06$, P = 0.81, respectively). Furthermore, parental host and exposure host did not interact in their effects on the proportion of males among adult offspring (type III $F_{9,87} = 0.58$, P = 0.81).

Host acceptance and suitability

While not quite significant at the 5% level, female *A. colemani* encountered *A. gossypii* at more than twice the rate at which they encountered *R. padi* (Figure 4; type III $F_{1,26} = 3.80$, P = 0.062). Larger females encountered hosts faster than smaller females (Figure 4; type III $F_{1,26} = 6.63$, P = 0.02). The host in which a female developed affected her dry mass ($F_{2,28} = 20.9$, $R^2 = 0.60$, P<0.001). At 52.2 ± 2.6 µg, female parasitoids from *S. graminum* were significantly larger than those from *R. padi* (39.0 ± 3.2 µg), which in turn, were significantly larger than those from *A. gossypii* (22.5 ± 2.5 µg) (Fisher's LSD: t = 2.05, P<0.05). Other than through effects on body size, parental host did not affect encounter rate (type III $F_{2,26} = 0.55$; P = 0.58).

Exposure host affected handling time: females spent more time handling *R. padi* than they did *A. gossypii* (10.1 ± 1.4 s vs. 5.1 ± 1.3 s; type III $F_{1,26} = 5.97$, P = 0.02). Neither a female's dry mass (type III $F_{1,26} = 0.95$, P = 0.34) nor the host species in which she developed (type III $F_{2,26} = 2.55$, P = 0.10) affected the speed with which she handled hosts.

Once an aphid was encountered, females oviposited in a higher proportion of *A. gossypii* than *R. padi* (0.83 ± 0.04 vs. 0.69 ± 0.04; type III $F_{1,26} = 5.50$, P = 0.027), but neither maternal dry mass (type III $F_{1,26} = 1.62$, P = 0.21) nor parental host (type III $F_{2,26} = 0.73$, P = 0.49) affected the proportion of encountered hosts accepted for oviposition.

Once a wasp egg was laid, the resulting progeny were over twice as likely to complete development and emerge as an adult in *A. gossypii* than in *R. padi* (0.76 ± 0.06 vs. 0.33 ± 0.06; type III $F_{1,26} = 22.5$, P<0.001). Again, neither maternal dry mass (type III $F_{1,26} = 2.20$, P = 0.15) nor parental host (type III $F_{2,26} = 1.25$, P = 0.30) affected the proportion of eggs that yielded adult progeny.

Unlike the previous experiment, the proportion of males among adult offspring did not differ between exposure hosts (type III $F_{1,23} = 0.41$, P = 0.53). However, the proportion of males was high (0.79) and many females (57%) produced no female progeny. In this experiment, we did not dissect a subset of females to determine whether they had indeed received sperm. Thus, the male-biased sex ratios and lack of effect of host species on sex ratio suggest that females were not as consistently mated in this experiment as in the previous experiment. When only those mothers that produced at least one daughter were considered, the proportion of males among adult offspring still was not affected by exposure host (type III $F_{1,8} = 1.34$, P = 0.28), although the mean proportion of males was 0.55. Like the previous experiment, neither maternal dry mass nor parental host affected the proportion of males among adult offspring (type III $F_{1,23} = 0.47$, P = 0.50 and type III $F_{2,23} = 0.20$, P = 0.82, respectively). Finally, we found no evidence for a differential survival of sons vs. daughters produced by mated or unmated females when exposed to either
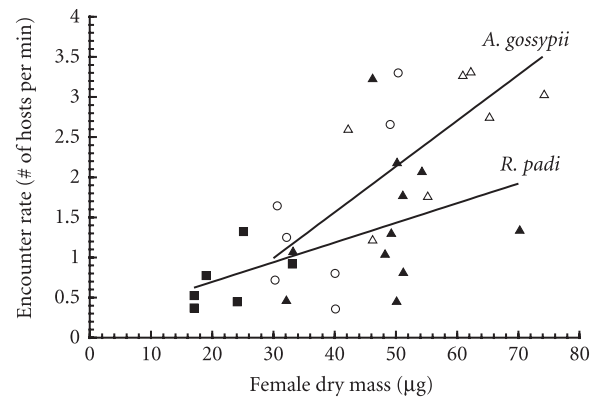

Figure 4 Encounter rate (number of hosts per min) vs. exposure host species and dry mass of ovipositing *Aphidius colemani* females ($F_{4,26} = 6.65$, P = 0.0008; see text for type III F statistics for individual source effects). Closed symbols represent encounter rate values for wasps exposed to *Rhopalosiphum padi*; open symbols represent encounter rate values for wasps exposed to *Aphis gossypii*. Regression lines are run through each set [*R. padi*: encounter rate = 0.25 +0.024 (hosts min^{-1}); *A. gossypii*: encounter rate = −0.71 +0.60 (hosts min^{-1})]. Symbol shape represents the parental host for searching female wasps: triangles represent *Schizaphis graminum*; circles represent *R. padi*; squares represent *A. gossypii*.

A. gossypii or *R. padi* (matedness × exposure host interaction: $F_{1,21} = 2.50$, $P = 0.13$). Offspring survival for females producing no daughters in *R. padi* was similar to offspring survival for females that produced at least one daughter ('mated': $37.5 \pm 4.8\%$ survival; 'unmated': $50.6 \pm 5.4\%$ survival). Likewise, offspring survival of females producing no daughters in *A. gossypii* was similar to offspring survival of mothers that produced at least one daughter ('unmated': $68.6 \pm 5.2\%$ survival; 'mated': $75.9 \pm 6.4\%$ survival).

Discussion

The results show that this population of *A. colemani* is poorly adapted to *R. padi* compared to the other three aphid species. Females exposed to *R. padi* produced fewer mummies and adult offspring than females exposed to the other three species. The second experiment showed that the difference in use of *A. gossypii* and *R. padi* resulted from how fast the ovipositing females encountered each host species, how fast each host species was handled, how readily each host species was accepted for oviposition, and how well the progeny survived in each host species. Taking these effects together, we would expect *A. colemani* females to produce about fourfold more offspring on *A. gossypii* than on *R. padi* over a fixed period of time, and this difference was what we observed in the first experiment. However, the estimates of encounter rate, proportion of hosts accepted for oviposition, and host suitability from the second experiment suggest that we should have seen 4–7-fold the number of offspring than was actually observed in the first experiment. It is possible that rates of encounter differed between the two experiments because of differences in cage design and the distribution of aphids on plants. Moreover, encounter rates may have differed due to size differences in *S. graminum* (and hence *A. colemani* females) between experiments 1 and 2. However, aside from its effect on maternal body size and thus encounter rate, the host species in which a female developed did not influence any of the measured host-use parameters.

Differences in the physical or chemical attributes of cotton and barley plants might explain differences in encounter rates between *A. gossypii* and *R. padi*. Differences in leaf shape or chemistry may affect aphid distribution on cotton vs. barley; this may in turn influence the foraging efficiency of *A. colemani* females. In one population of *A. colemani*, females showed a foraging preference for the host plant on which they had emerged (Storeck et al., 2000). Host plant species may also influence the development of parasitoids in different aphid species. Some populations of aphids exhibit physiologically based resistance to the development of *A. ervi* eggs (Henter & Via, 1995). Differences in resistance to parasitism between *A. gossypii* and *R. padi*

might be determined by the different effects of host plant species on aphid physiology. However, we saw no evidence of reduced survival of *A. colemani* in *S. graminum*, even though this aphid was exposed on barley like *R. padi*. Likewise, Hufbauer & Via (1999) showed that differences in pea aphid susceptibility to parasitism by *A. ervi* did not arise from differences in host plant species.

Male-biased sex ratios are often associated with poor quality hosts (King, 1993; Godfray, 1994). When female fitness correlates are more strongly influenced by host quality, ovipositing females should allocate daughters to higher quality hosts and sons to lower quality hosts. A higher proportion of males emerging from *R. padi* than from the other three aphid species further suggests that *R. padi* is a poor quality host for this wasp population. Either mothers tend to lay more male-biased sex ratios in *R. padi*, or female survival is lower in *R. padi* than in the other species of aphids. Unfortunately, many of the females used in the second experiment were apparently unmated, producing only sons. In addition, the probability of mortality, particularly in *R. padi*, was high, preventing us from directly assessing the primary sex ratio. When the survivorship data were reanalyzed ignoring the families where only sons were produced, we found that similar proportions of sons emerged from both *A. gossypii* and *R. padi*; it is unclear why these findings are contrary to those of the first experiment. Knowledge of the sex ratio laid by the mother is needed before we can distinguish between the possibilities of differential mortality and sex allocation responses of females.

Despite being a poor quality host in terms of the number of offspring produced, encounter rate, handling time, and the likelihood of acceptance and survivorship, *R. padi* appears to be a more favorable host in terms of the larger size of individuals that do develop, compared to those from *A. gossypii*. This represents a trade-off between larval survival and adult body size when developing in *A. gossypii* vs. *R. padi*. Given that individuals are larger, and presumably have higher fitness, when they develop in *R. padi*, why do more males emerge from *R. padi* than from *A. gossypii*? If daughters are less likely to successfully develop in *R. padi* than sons, ovipositing females will be selected to lay a higher proportion of sons in *R. padi*. On the other hand, if there is no differential survival of males and females in *R. padi*, sex allocation is not expected to be influenced by the low probability of survival in *R. padi*. However, if sperm is limited, a mother should oviposit fertilized eggs (i.e., daughters) in *A. gossypii* where the probability of survival is greater. Although not significantly different, 50% of the progeny produced by presumably unmated females survive in *R. padi*, whereas only 38% of the progeny produced by mated females survive in *R. padi*. While this is mildly suggestive of differential mortality in

R. padi, more definitive experiments examining the sex ratio at oviposition are required.

Ovipositing females should accept host species in which their offspring have a higher probability of survival. While it is well known that females respond to variations in host quality by modifying host acceptance, clutch size, and sex allocation, most of these studies have involved intraspecific variations in host quality (Godfray, 1994). Our results show that females from this population of *A. colemani* do indeed oviposit preferentially in host species that provide higher survival for their offspring, although the preferred host species for oviposition yields smaller and presumably less fit individuals. Such a correlation between oviposition and offspring survival would help to explain the accumulating evidence for interpopulation differences in host use observed in other species of *Aphidius*, as well as in other parasitoid families (e.g., Stary, 1983; Pungerl, 1984; Takada & Tada, 2000). However, studies of oviposition vs. progeny fitness in phytophagous insects have yielded equivocal findings across species (Barbosa, 1988; Courtney & Kibota, 1989; Thompson & Pellmyr, 1991). While some species prefer to oviposit on plants that result in higher larval performance (e.g., Singer et al., 1988), by no means all do (e.g., Thompson, 1996). A variety of factors, including 'enemy-free space' (e.g., Atsatt, 1981; Jermy, 1988; Gratton & Welter, 1999), and the effects of plant chemistry on host plant location (Ehrlich & Murphy, 1988; Schultz, 1988) may obscure the relationship between oviposition and offspring performance. Similar constraints may operate on parasitoid oviposition preferences across potential host species. Studies of a variety of parasitoid species, designed to measure host encounter, host acceptance, and host suitability, are needed before we can say whether the pattern of oviposition preference and larval performance observed in *A. colemani* recurs among other species of parasitoids.

Our results also have implications for biological control introductions. Although the reported host range for *A. colemani* is very broad (Stary, 1975; Kalina & Stary, 1976; Takada, 1998), not all wasp populations will provide equal levels of control against all target aphid species.

Acknowledgements

References

van Alphen JJM & Janssen ARM (1982) Host selection by *Asobara tabida* Nees (Braconidae; Alysiinae), a larval parasitoid of fruit inhabiting *Drosophila* species. II. Host species selection. Netherlands Journal of Zoology 32: 215–231.

Askew RR & Shaw MR (1986) Parasitoid communities: their size, structure and development. Insect Parasitoids (ed. by JK Waage & D Greathead), pp. 225–264. Academic Press, London.

Atanassova P, Brookes CP, Loxdale HD & Powell W (1998) Electrophoretic study of five aphid parasitoid species of the genus *Aphidius* (Hymenoptera: Braconidae), including evidence for reproductively isolated sympatric populations and a cryptic species. Bulletin of Entomological Research 88: 3–13.

Atsatt PR (1981) Lycaenid butterflies and ants: selection for enemy-free space. American Naturalist 188: 638–654.

Barbosa P (1988) Some thoughts on 'the evolution of host range'. Ecology 69: 912–915.

Cameron PJ, Powell W & Loxdale HD (1984) Reservoirs for *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae). Bulletin of Entomological Research 74: 647–656.

Chau A & Mackauer M (2001) Preference of the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae) for different aphid species: female choice and offspring survival. Biological Control 20: 30–38.

Courtney SP & Kibota TT (1989) Mother doesn't know best: selection of hosts by ovipositing insects. Insect–Plant Interactions (ed. by EA Bernays), Vol. II, pp. 161–188. CRC Press, Boca Raton, FL.

DeBach P & Rosen D (1991) Biological Control by Natural Enemies, 2nd edn. Cambridge University Press, Cambridge, UK.

Ehrlich PR & Murphy DD (1988) Plant chemistry and host range in insect herbivores. Ecology 69: 908–909.

Futuyma DJ & Moreno G (1988) The evolution of ecological specialization. Annual Review of Ecology and Systematics 19: 207–233.

Godfray HCJ (1994) Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, Princeton.

Gratton C & Welter SC (1999) Does 'enemy-free space' exist? Experimental host shifts of an herbivorous fly. Ecology 80: 773–785.

Henter HJ & Via S (1995) The potential for coevolution in a host-parasitoid system. I. Genetic variation within an aphid population in susceptibility to a parasitic wasp. Evolution 49: 427–438.

Hopper KR (2000) Research needs concerning non-target impacts of biological control introductions. Evaluating Indirect Ecological Effects of Biological Control (ed. by E Wajnberg, JK Scott & PC Quimby), pp. 39–56. CABI Bioscience, London.

Hopper KR, Coutinot D, Chen K, Mercadier G, Halbert SE, Kazmer DJ, Miller RH, Pike KS & Tanigoshi LK (1998) Exploration for natural enemies to control *Diuraphis noxia* in the United States. A Response Model for an Introduced Pest – The Russian Wheat Aphid (ed. by SS Quissenbery & FB Peairs), pp. 166–182. Entomological Society of America, Lanham, MD.

Hufbauer RA & Via S (1999) Evolution of an aphid–parasitooid interaction: variation in resistance to parasitism among aphid populations specialized on different plants. Evolution 53: 1435–1445.

Jermy T (1988) Can predation lead to narrow food specialization in phytophagous insects? Ecology 69: 902–904.

Kalina V & Stary P (1976) A review of the aphidophagous Aphelinidae (Hymenoptera, Chalcidoidea), their distribution and host range in Europe. Studia Entomologica Forestalia (Praha, Czechoslovakia) 2: 143–170.

King BH (1993) Sex ratio manipulation by parasitoid wasps. Evolution and Diversity of Sex Ratio in Insects and Mites (ed. by DL Wrensch & MA Ebbet), pp. 418–441. Chapman & Hall, New York.

Lynch M & Gabriel W (1987) Environmental tolerance. American Naturalist 129: 283–303.

Mescheloff M & Rosen D (1990) Biosystematic studies on the Aphidiidae. 4. The genera *Pauesia*, *Diaretus*, *Aphidius* and *Diaeretiella*. Israel Journal of Entomology 24: 51–91.

Messing RH & Rabasse JM (1995) Oviposition behaviour of the polyphagous aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). Agriculture, Ecosystems and Environment 52: 13–17.

Nemec V & Stary P (1983) Elpho-morph differentiation in *Aphidius ervi* Hal. biotype on *Microlophium carnosum* (Bckt.) related to parasitization on *Acyrthosiphon pisum* (Harr.) (Hym., Aphidiidae) Zeitschrift für Angewandte Entomologie 95: 524–530.

Pike KS, Stary P, Miller T, Allison D, Graf G, Boydston L, Miller R & Gillespie R (1999) Host range and habitats of the aphid parasitoid *Diaretiella rapae* (Hymenoptera: Aphiididae) in Washington State. Environmental Entomology 28: 61–71.

Powell W & Wright AF (1988) The abilities of the aphid parasitoids *Aphidius ervi* Haliday and *A. rhopalosiphum* De Stefani Perez (Hymenoptera: Braconidae) to transfer between different known host species and the implications for the use of alternative hosts in pest control strategies. Bulletin of Entomological Research 78: 683–693.

Pungerl NB (1984) Host preferences of *Aphidius* (Hymenoptera: Aphidiidae) populations parasitising pea and cereal aphids (Hemiptera: Aphididae). Bulletin of Entomological Research 74: 153–161.

Schultz JC (1988) Many factors influence the evolution of herbivore diets, but plant chemistry is central. Ecology 69: 896–897.

Simberloff D & Stiling P (1996) How risky is biological control? Ecology 77: 1965–1974.

Singer MC, Ng D & Thomas CD (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. Evolution 42: 977–985.

Stary P (1975) *Aphidius colemani* Viereck: its taxonomy, distribution and host range (Hymenoptera, Aphidiidae). Acta Entomologica Bohemoslovaka 72: 156–163.

Stary P (1983) Colour patterns of adults as evidence on *Aphidius ervi* biotypes in field environments (Hymenoptera, Aphidiidae). Acta Entomologica Bohemoslovaka 80: 377–384.

Storeck A, Poppy GM, van Emden HF & Powell W (2000) The role of plant chemical cues in determining host preference in the generalist aphid parasitoid *Aphidius colemani*. Entomologia Experimentalis et Applicata 97: 41–46.

Strand MR (1986) The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. Insect Parasitoids (ed. by JK Waage & D Greathead), pp. 97–136. Academic Press, London.

Takada H (1998) A review of *Aphidius colemani* (Hymenoptera: Braconidae; Aphidiinae) and closely related species indigenous to Japan. Applied Entomology and Zoology 33: 59–66.

Takada H & Tada E (2000) A comparison between two strains from Japan and Europe of *Aphidius ervi*. Entomologia Experimentalis et Applicata 97: 11–20.

Tardieux I & Rabasse JM (1986) Host-parasite interrelationships in the case of *Aphidius colemani*. Ecology of Aphidophaga. (ed. by I Hodek), pp. 125–130. Academia, Praha, Czechoslovakia.

Tardieux I & Rabasse JM (1990) Role of some epigenetic factors influencing the host suitability of *Myzus persicae* for the parasitoid *Aphidius colemani*. Entomologia Experimentalis et Applicata 54: 73–80.

Thompson JN (1996) Trade-offs in larval performance on normal and novel hosts. Entomologia Experimentalis et Applicata 80: 133–139.

Thompson JN & Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. Annual Review of Entomology 36: 65–89.

Vet LEM & Groenewold AW (1990) Semiochemicals and learning in parasitoids. Journal of Chemical Ecology 16: 3119–3135.

Via S & Lande R (1985) Genotype–environment interaction and the evolution of phenotypic plasticity. Evolution 39: 505–522.